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Citation: Puts, David, Hill, Alexander, Bailey, Drew, Walker, Robert, Rendall, Drew, Wheatley, John, Welling, Lisa, Dawood, Khytam, Cárdenas, Rodrigo, Burriss, Robert, Jablonski, Nina, Shriver, Mark, Weiss, Daniel, Lameira, Adriano, Apicella, Coren, Owren, Michael, Barelli, Claudia, Glenn, Mary and Ramos-Fernandez, Gabriel (2016) Sexual selection on male vocal fundamental frequency in humans and other anthropoids. *Proceedings of the Royal Society B: Biological Sciences*, 283 (1829). p. 20152830. ISSN 0962-8452

Published by: The Royal Society

URL: <http://dx.doi.org/10.1098/rspb.2015.2830> <<http://dx.doi.org/10.1098/rspb.2015.2830>>

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1

2 **Sexual selection on male vocal fundamental frequency in humans and**  
3 **other anthropoids**

4 Short title: Sexual selection and primate vocalization frequencies

5

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32 **Abstract**

33 In many primates, including humans, the vocalizations of males and females differ dramatically,  
34 with male vocalizations and vocal anatomy often seeming to exaggerate apparent body size.  
35 These traits may be favored by sexual selection because low-frequency male vocalizations  
36 intimidate rivals and/or attract females, but this hypothesis has not been systematically tested  
37 across primates, nor is it clear why competitors and potential mates should attend to  
38 vocalization frequencies. Here we show across anthropoids that sexual dimorphism in  
39 fundamental frequency ( $F_0$ ) increased during evolutionary transitions toward polygyny, and  
40 decreased during transitions toward monogamy. Surprisingly, humans exhibit greater  $F_0$  sexual  
41 dimorphism than any other ape. We also show that low- $F_0$  vocalizations predict perceptions of  
42 men's dominance and attractiveness, and predict hormone profiles (low cortisol and high  
43 testosterone) related to immune function. These results suggest that low male  $F_0$  signals  
44 condition to competitors and mates, and evolved in male anthropoids in response to the  
45 intensity of mating competition.

46 **Introduction**

47           Explaining why sexual dimorphisms evolve is central to understanding the evolution of  
48 primate mating systems and social organization. In many primate species, the vocalizations of  
49 males and females differ dramatically, with male vocalizations and vocal anatomy often seeming  
50 to exaggerate the appearance of body size (1-7). Among humans, men's approximately 60%  
51 longer vocal folds (8, 9) contribute to an average rate of vocal fold vibration during phonation  
52 (fundamental frequency,  $F_0$ ) that is about five standard deviations below women's (5). To human  
53 listeners, utterances lower in  $F_0$  are perceived as being deeper in pitch and as emanating from  
54 larger individuals (10, 11). The evolutionary reasons for such apparent size exaggeration have  
55 been the subject of speculation since Darwin noted the pubertal enlargement of male vocal  
56 structures and their intensified employment during the breeding season in many mammals (12).

57           Some have suggested that male vocalizations evolve to intimidate male competitors  
58 and/or attract mates (6, 13). For example, among orangutans, lower-ranking males avoid long  
59 calls given by higher-ranking males (14), suggesting that acoustic cues convey threat-potential  
60 to conspecifics. Several studies in humans suggest that  $F_0$  has relevance under both inter- and  
61 intrasexual competition: Experimentally lowering  $F_0$  increases perceptions of men's dominance  
62 and attractiveness (11, 15), and raising  $F_0$  increases women's vocal attractiveness (16, 17).  
63 However, little is known about whether these effects persist in unmanipulated speech when  $F_0$   
64 and other acoustic parameters vary naturally and simultaneously.

65           Moreover, it is unclear why  $F_0$  should signal formidability to same-sex competitors or  
66 mate value to potential mates;  $F_0$  is only weakly associated with body size (5, 7, 18-20) and  
67 perhaps strength (5, 21) in humans, although  $F_0$  may be modulated according to relative  
68 formidability (22) and mate quality (23, 24). Steroid hormones may provide a link between  $F_0$   
69 and condition. Growing evidence indicates that glucocorticoids such as the stress hormone  
70 cortisol negatively interact with testosterone in affecting both immune function and the  
71 expression of secondary sex traits (25-27). Infection stimulates cortisol production (28), which

72 downregulates androgen receptors and inhibits the action of testosterone on target tissues (29-  
73 33). Hence, testosterone should be more potent in individuals in good condition with low  
74 immune system activation. In humans, positive relationships between testosterone and immune  
75 response to a vaccine (34), and between testosterone and both facial attractiveness (34) and  
76 dominance (35), were stronger in males with low cortisol. Furthermore, the interactive effect of  
77 testosterone and cortisol on attractiveness was mediated by immune function, supporting the  
78 stress-linked immunocompetence handicap hypothesis (SL-ICHH) that testosterone-related  
79 traits that interact with cortisol are linked to immunocompetence (34). Although previous studies  
80 have found negative relationships between men's testosterone and  $F_0$  (5, 20), it is unknown  
81 whether testosterone and cortisol negatively interact in predicting  $F_0$ , as the SL-ICHH would  
82 suggest if  $F_0$  reflects underlying condition.

83 More generally, scant evidence exists to support a role for sexual selection in shaping  $F_0$   
84 and other vocal sexual dimorphisms across primates (6), and there are plausible alternative  
85 hypotheses:  $F_0$  dimorphism may represent a byproduct of selection for greater male size or  
86 long-distance transmission of male calls (36), or reflect selection for sex identification. The latter  
87 two hypotheses predict relationships between habitat and  $F_0$  dimorphism. In general, open,  
88 terrestrial habitats are poor acoustic environments in which sounds greatly attenuate over  
89 distance compared with arboreal habitats. This is particularly true for the heights at which each  
90 habitat's primate residents tend to communicate and for lower frequency sounds (37). Thus, all  
91 else equal, selection for long-distance transmission of male calls should tend to produce  
92 relatively lower frequency male calls in arboreal environments than in terrestrial ones (for  
93 caveats, see Discussion). Likewise, because primates are both more visible and more sexually  
94 dimorphic in terrestrial species than in arboreal ones (38), selection for sex identification should  
95 favor greater  $F_0$  dimorphism in arboreal species.

96 Here, we report the results of three studies designed to clarify the evolution of sexual  
97 dimorphism in  $F_0$ . In Study 1, we examined the evolution of  $F_0$  dimorphism as a function of

98 mating system, as well as body mass dimorphism and habitat, across anthropoid primates.  
99 Studies 2 and 3 focused on humans. Not only are humans of special interest, but they are also  
100 highly useful as a model organism: There is strong evidence implicating sexual selection in the  
101 evolution of human  $F_0$  (39, 40), as well as a unique richness to the data available for addressing  
102 the questions outlined above, as we detail below. In Study 2, we tested the stimulus-response  
103 properties of  $F_0$  on intrasexual competitiveness in humans by examining the independent  
104 contributions of  $F_0$  and other acoustic parameters related to assessments of attractiveness and  
105 dominance. In Study 3, we explored the indexical value of  $F_0$  by testing the SL-ICHH prediction  
106 that  $F_0$  will be more strongly linked to testosterone in individuals with low cortisol.

107

## 108 **Study 1: $F_0$ across anthropoid primates**

### 109 **Methods**

110 Please refer to *SI Materials and Methods* for additional details.

111 We obtained recordings of nonhuman primate calls from our own fieldwork and by  
112 contacting other primatologists. From these, we selected 1721 files, such that each was without  
113 substantial background noise and was produced by a single individual of known species, sex,  
114 and adult status. The acoustic properties of primate calls vary across call types and contexts  
115 (13). We chose to utilize measurements across all available call types (but see also  
116 Supplementary Results) rather than, for example, selecting only calls believed to be analogous  
117 across species, or only calls shared between males and females. Our reasoning was that  
118 averaging across call types should maximize our ability to capture information about the  
119 physical properties of the sound source (e.g., vocal fold length and thickness), especially if  
120 some call types may provide more information than others. If  $F_0$  is driven by underlying  
121 anatomy—as it is fundamentally—then any influence on  $F_0$  should be manifest similarly across  
122 call types, even if not specifically adapted to be, because the same anatomy supports the  
123 production of all calls. Although it is possible that some other special mechanism of vocal fold

124 action is in play for some calls (e.g., loud calls compared to close calls), this is not a given and  
125 certainly cannot be assumed a priori. Moreover, it is unclear whether call types are truly  
126 analogous across species, which complicates comparisons of only a particular call type or set of  
127 types. In addition, the repertoire shared between males and females can be very limited in some  
128 primate species, occasionally down to one call type, as in the orangutan. Finally, we do not  
129 know of any reason that our sampling procedures would have systematically biased our sample,  
130 and the size of our sample—the largest ever compiled for this type of research—should reduce  
131 any bias due to random sampling.

132 Files were measured as uncompressed .WAV or .AIFF files using the acoustic analysis  
133 software Praat version 5.3.  $F_0$  was measured from each file by identifying in the raw waveform a  
134 segment in which cycles were clearly discernible. Cycles were counted along this segment up to  
135 20 cycles, and then divided by the duration of the interval to calculate  $F_0$ . This procedure was  
136 repeated for a second segment, if possible (78% of files,  $n = 1343$ ). Mean  $F_0$  values from each  
137 recording were averaged with all other mean  $F_0$  values per sex to arrive at separate male and  
138 female  $F_0$  averages for each species (Table S2). Between-segment reliability was high for files  
139 with two measurable segments (Cronbach's  $\alpha = 0.973$ ). First segments of a randomly chosen  
140 11% of files ( $n = 184$ ) were re-measured to determine intra-measurer reliability, which was very  
141 high (Cronbach's  $\alpha = 1.000$ ). Body size, habitat, and mating system were obtained from the  
142 literature (Table S2).

143 Mating system was utilized as a proxy for the intensity of sexual selection (41, 42). We  
144 categorized mating system as monogamous, promiscuous, or polygynous (43) rather than using  
145 an interval-level measure such as socionomic sex ratio, as such measures often vary widely  
146 within species and hold uncertain relationships to the intensity of intermale competition (41, 44,  
147 45). Promiscuity differs from monogamy and polygyny in that females far more frequently  
148 copulate with multiple males in promiscuous species. Although evidence suggests intermediate  
149 levels of male contest competition in promiscuous species, the ability of males to monopolize



150 females varies widely (46), other mechanisms of sexual selection such as sperm competition  
151 are more salient (47, 48), and the degree of sexual dimorphism relative to monogamous or  
152 polygynous species varies widely by trait (47). Such apparent diversity in the mechanisms and  
153 intensity of sexual selection, as well as their influence on sexual dimorphism, precludes  
154 straightforward predictions regarding  $F_0$  dimorphism in promiscuous species. By contrast,  
155 predictions regarding monogamous and polygynous species are clearer: In polygynous species,  
156 some males are able to monopolize multiple mates, whereas in monogamous species, males do  
157 not, leaving fewer males unmated. Hence, sexual selection—particularly, intrasexual selection—  
158 tends to be more intense in polygynous than in monogamous primates, which are less  
159 dimorphic in size and weaponry (47). Dimorphism in  $F_0$  was therefore predicted to increase  
160 during evolutionary transitions toward polygyny and decrease during transitions toward  
161 monogamy.

162 Habitat was categorized as arboreal, terrestrial, or arboreal/terrestrial. We conducted  
163 phylogenetically-informed analyses using a consensus phylogeny for all species represented in  
164 our sample (49; Fig. 1) and assessed correlated evolution among our variables with  
165 phylogenetic generalized least squares regression using the caper package, v.0.5.2, in R (50).

166

## 167 **Results**

168 Across analyses,  $F_0$  and  $F_0$  dimorphism exhibited strong phylogenetic signals ( $\lambda > 0.8$ ).  
169 In general, New World primates showed little sexual dimorphism in  $F_0$ , averaging a mean  $F_0$   
170 dimorphism (male  $F_0$ /female  $F_0$ ) of 1.05 across 7 species, while male cercopithecines averaged  
171 half of the  $F_0$  of females (mean  $F_0$  dimorphism = 0.48 across 10 species). With a similar  $F_0$   
172 dimorphism of 0.51, humans surprisingly exhibited the greatest dimorphism that we measured in  
173 any ape.

174 We tested whether increases in body size predict decreases in  $F_0$  across species for  
175 each sex. Previous studies relied on published acoustic data measured using varying

176 methodologies and either averaged male and female measurements (51) or included only males  
177 (36). In our data, body mass negatively predicted  $F_0$  (both variables natural log-transformed) in  
178 males and females (Table 1). These results suggest that body size constrains the evolution of  
179 primate call frequencies in both sexes (51).

180 We then regressed  $F_0$  dimorphism on mating system, controlling for body size  
181 dimorphism (male mass/female mass). Because diversity in the mechanisms and intensity of  
182 sexual selection precludes straightforward predictions regarding  $F_0$  dimorphism in promiscuous  
183 species (see above), we excluded promiscuous species from this analysis; however,  
184 promiscuous species appear intermediate in  $F_0$  dimorphism (Fig. 2a). We found that greater  $F_0$   
185 dimorphism evolves in transitions to polygyny than in transitions to monogamy (Table 1, Fig.  
186 2c). In this model, changes toward greater  $F_0$  dimorphism also tended to be accompanied by  
187 decreases in body size dimorphism. Humans were treated as polygynous (52) and exhibited  $F_0$   
188 dimorphism that was outside the range of monogamous species (Fig. 2a); however, we  
189 obtained similar results when humans were treated as monogamous, or excluded from the  
190 analysis (Table 1).

191 Finally, we tested the relationship between  $F_0$  dimorphism and habitat. If male  
192 vocalizations are selected primarily to propagate over distance, or if  $F_0$  dimorphism evolves  
193 primarily for sex discrimination, then arboreal species should tend to exhibit relatively lower  
194 male  $F_0$  than terrestrial species. We found the reverse: Arboreal primates showed less  $F_0$   
195 dimorphism than terrestrial primates when  $F_0$  dimorphism was regressed on habitat and mass  
196 dimorphism (Table 1).

197

## 198 **Study 2: $F_0$ , dominance, and attractiveness in humans**

### 199 **Methods**

200 Please refer to *SI Materials and Methods* for additional details.

201 Two hundred fifty-eight female (mean age  $\pm$  s.d. = 20.0  $\pm$  1.6 y) and 175 male (20.1  $\pm$   
202 1.7 y) students from Michigan State University provided written consent to participate in this  
203 study approved by the university's Institutional Review Board. Participants were recorded  
204 reading a standard voice passage (53) in an anechoic, soundproof booth using a Shure SM58  
205 vocal cardioid dynamic microphone (frequency response: 50-15,000 Hz) positioned at  
206 approximately 30 degrees and 9.5 cm from the speaker's mouth, and connected to a desktop  
207 computer via a Sound Devices USBPre 2 preamplifier. Voices were recorded in mono at a  
208 sampling rate of 44,100 Hz and 16-bit quantization, and saved as uncompressed .WAV files.  
209 Recordings were rated by 558 female (19.1  $\pm$  2.4 y) and 568 male (19.4  $\pm$  1.8 y) students from  
210 The Pennsylvania State University. Each female recording was rated by 15 men for  
211 attractiveness for short- and long-term romantic relationships using 7-point Likert scales. Each  
212 male recording was rated by 15 men for dominance (7-point scale) and 15 women for short- and  
213 long-term attractiveness. Ratings were averaged to produce composite ratings of short- and  
214 long-term attractiveness for each recording, and dominance for each male recording.

215 Recordings were analyzed using Praat version 5.3 for mean  $F_0$ , standard deviation in  $F_0$   
216 across the utterance ( $F_0$ -SD), duration, number of voice breaks, harmonics, four measures of  
217 jitter (cycle-to-cycle variation in  $F_0$ ), and five measures of shimmer (cycle-to-cycle variation in  
218 amplitude) using the "voice report" function in Praat (Table S3). Pitch floors were set to 75 Hz  
219 and 100 Hz, and pitch ceilings were 300 Hz and 500 Hz, for men and women, respectively.  
220 Otherwise, default settings were used. We also measured the first four formant frequencies ( $F_1$ -  
221  $F_4$ , Table S3). Formants were measured at each glottal pulse, averaged across measurements,  
222 and then used to compute formant position ( $P_f$ ), the average standardized formant value for the  
223 first four formants (5).

224 Using SPSS v.22, we performed a separate male and female principal components  
225 analyses to reduce the number of acoustic control variables (SI Materials and Methods, Table

226 S4), and we utilized multiple regression to examine the effects of acoustic parameters on  
227 perceptual variables.

228

## 229 **Results**

230  $F_0$  predicted men's perceived dominance to heterosexual male listeners ( $\beta = -0.43, p <$   
231  $0.0001$ ) and attractiveness to heterosexual female listeners for both prospective short-term ( $\beta =$   
232  $-0.36, p < 0.001$ ) and long-term ( $\beta = -0.32, p = 0.001$ ) romantic relationships (Table S5). When  
233 perceived dominance and short-term attractiveness were entered into a multiple regression to  
234 predict men's  $F_0$  (model  $F_{2,171} = 12.99, p < 0.0001, R^2 = 0.13$ ), dominance negatively predicted  
235  $F_0$  ( $\beta = -0.30, p = 0.001$ ), but short-term attractiveness did not ( $\beta = -0.09, p = 0.314$ ), suggesting  
236 a stronger role for male contests than female choice in shaping men's  $F_0$ .  $F_0$  did not predict  
237 women's attractiveness to men for either short- ( $\beta = 0.03, p = 0.695$ ) or long-term ( $\beta = -0.03, p =$   
238  $0.722$ ) relationships when other acoustic parameters were statistically controlled (Table S5).  
239 These results are thus more consistent with sexual selection (primarily intrasexual selection) on  
240 males, rather than intersexual selection on females, influencing the evolution of human  $F_0$   
241 dimorphism.

242

## 243 **Study 3: $F_0$ and hormonal profiles in humans**

### 244 **Methods**

245 Please refer to *SI Materials and Methods* for additional details.

246 Participants from The Pennsylvania State University provided written consent to  
247 participate in this study approved by the university's Institutional Review Board. Fifty-three  
248 normally-cycling women (mean age  $\pm$  s.d. =  $19.4 \pm 1.6$  y) and 62 men ( $19.9 \pm 2.0$  y) were  
249 recorded in an anechoic recording booth in a quiet room (Sample 1), and 58 men ( $19.9 \pm 1.2$  y)  
250 were recorded in a quiet room (Sample 2) using the equipment and methods in Study 2 above.

251 Participants rinsed their mouths with water before providing two saliva samples of 1-2 ml  
252 each via passive drool approximately 30 (Sample 1) or 20 (Sample 2) min apart. From each  
253 sample, 0.5 ml of saliva was aliquotted into a third tube, which was shaken and then frozen at -  
254 20°C until analysis by the Johns Hopkins Center for Interdisciplinary Salivary Bioscience  
255 Research (Baltimore, MD) using Salimetrics® kits. Samples were analyzed in duplicate via  
256 enzyme immunoassay. Duplicates correlated highly for both cortisol and testosterone (all  $r \geq$   
257 0.97,  $p < 0.0001$ ), and were consequently averaged. For cortisol assays, sensitivity is  $<0.003$   
258  $\mu\text{g/dL}$ , and average intra-assay coefficient of variation is 3.5%. For testosterone assays,  
259 sensitivity is  $<1.0$  pg/mL, and average intra-assay coefficient of variation is 4.6%.

260 Hormone data were natural log-transformed to correct skew prior to analysis. We utilized  
261 multiple regression to examine the effects of cortisol and testosterone on  $F_0$  and statistically  
262 controlled for diurnal decreases in cortisol and testosterone (54), but results were similar without  
263 controlling for these effects (Table S6, Figs. S1, S2).

264

## 265 Results

266 In women,  $F_0$  was unrelated to cortisol, testosterone, and their interaction (Table S6).  
267 However, in both male samples, cortisol and testosterone interacted in predicting  $F_0$  (Sample 1:  
268  $\beta = 0.36$ ,  $p = 0.007$ ; Sample 2:  $\beta = 0.28$ ,  $p = 0.033$ ; Table S6) such that testosterone was  
269 negatively related to  $F_0$  only in low-cortisol men (median split for cortisol; Sample 1: partial  $r = -$   
270 0.44,  $p = 0.018$ ; Sample 2: partial  $r = -0.40$ ,  $p = 0.034$ ; see also Fig. S2). This pattern of  
271 relationships between hormones and a putative sexually selected trait has been found to  
272 indicate men's immune function (34), as well as attractiveness (34) and dominance (35), and is  
273 consistent with the SL-ICHH (34).

274

## 275 Discussion

276 Our data supported the sexual selection hypothesis:  $F_0$  dimorphism increased with  
277 evolutionary changes toward polygyny and decreased with transitions toward monogamy across  
278 anthropoid primates. Although our primary analyses averaged across call types in order to  
279 maximize data, we also examined patterns of  $F_0$  dimorphism across mating systems using only  
280 those calls for which we had examples from both sexes (SI Results, Fig. S3). Patterns were  
281 similar across analyses, indicating that the observed pattern in our primary results does not  
282 merely reflect sex differences in the use of particular call types, which may differ in  $F_0$ . Our data  
283 also indicate that sex differences in  $F_0$  result mainly from selection on males rather than  
284 females: We observed greater  $F_0$  dimorphism in polygynous species, where male sexual  
285 selection is stronger, and  $F_0$  affected components of men's but not women's mating success.  
286 These results thus provide a plausible explanation for the prior finding that  $F_0$  predicted men's  
287 but not women's reproductive success among Hadza foragers (55). If low  $F_0$  augments male  
288 reproductive success by increasing access to mates in some other anthropoids, as appears to  
289 be the case in humans, then we would expect males to evolve relatively lower  $F_0$  when mating  
290 competition intensifies during transitions to polygyny, as we found.

291 By contrast,  $F_0$  dimorphism appears unlikely to be a byproduct of greater male size: With  
292 mating system controlled,  $F_0$  dimorphism decreased with relative male size. Although  $F_0$   
293 dimorphism likely facilitates sex identification, if it evolves primarily for this function, then one  
294 might expect it to be greater in arboreal species where visibility is obscured, and in  
295 monogamous species where the sexes are otherwise less dimorphic (38), yet in both cases we  
296 found the opposite.

297 Previous work indicates that lower frequency male loud calls are selected for  
298 propagation over distance (36), but our finding that male  $F_0$  is relatively lower in terrestrial  
299 species than in arboreal species suggests that selection for long-distance male calls is not the  
300 only or primary influence on  $F_0$  dimorphism across species' vocal repertoires. Lower frequencies  
301 should, *ceteris paribus*, aid long-distance transmission to a greater degree in arboreal habitats

302 than in terrestrial ones for the heights at which primates normally communicate. Although we  
303 view our measure of environmental influence on acoustic transmission (arboreal vs. terrestrial)  
304 as a safe parsing for such a broad sample encompassing a panoply of subtly different habitat  
305 types, it is admittedly crude, and environmental effects on acoustic transmission are complex.  
306 Other variables such as type of call, location in an arboreal environment, and ambient noise are  
307 likely to play a role (37), and an exploration of these influences should be taken up more fully as  
308 more precise data accumulate. However, such possible environmental influences might be  
309 expected to weaken any relationship between  $F_0$  dimorphism and arboreal vs. terrestrial habitat  
310 rather than producing an effect that is opposite the predicted direction. Our results thus  
311 challenge the hypothesis that overall  $F_0$  dimorphism primarily evolves when male calls are  
312 selected for long-distance transmission, and our findings are more consonant with elevated  
313 male-male competition in terrestrial compared with arboreal species (56, 57).

314         Inspection of Fig. 1 indicates an increase in  $F_0$  dimorphism from the last common  
315 ancestor of the apes to modern humans, culminating in humans exhibiting the greatest  $F_0$   
316 dimorphism of all apes. These results contrast sharply with moderate human body mass  
317 dimorphism and negligible canine length dimorphism, which some have suggested indicate  
318 weak sexual selection in ancestral humans (58). However, unlike other primates, in humans,  
319 female adiposity greatly exceeds that of males, producing modest overall mass dimorphism  
320 despite the fact that males possess 60% more muscle mass, and men fight with handheld  
321 weapons and fists rather than teeth in combat (57, 59). These unique features preclude  
322 conclusions about the strength of human sexual selection based on overall mass or canine size  
323 dimorphism (60, 61). Yet, if mating competition also tends to decrease male  $F_0$  relative to  
324 female  $F_0$  across primates, then  $F_0$  dimorphism has the potential to elucidate human sexual  
325 selection in ways that comparisons of body mass or canine size cannot. Our results suggest  
326 that, despite widespread pair-bonding and contrary to some claims (58, 62), ancestral human  
327 mating should not be viewed as fundamentally monogamous (52).

328           When phylogeny and mating system were statistically controlled, evolutionary changes  
329 toward greater  $F_0$  dimorphism were associated with changes toward less body size dimorphism  
330 and vice versa. Perhaps where mates are won mainly through direct fighting, males receive less  
331 benefit from exaggerating size acoustically and must instead invest in mass that is useful in  
332 contests. Conversely, acoustic threats and displays may be more effective when body mass or  
333 fights are especially costly, or where female choice is more important to male fitness. In  
334 humans, male  $F_0$  was indeed important in mate attraction, yet  $F_0$  more strongly predicted  
335 perceptions of men's dominance, consistent with previous experimental evidence (22, 39).  
336 Masculinity in men's faces is similarly perceived as aggressive across human societies,  
337 whereas the influence on attractiveness is more variable in magnitude and direction (63). While  
338 such male traits appear better designed to function in male contests than in female choice (57),  
339 it remains possible that female choice is relatively more important in humans compared to other  
340 polygynous primates, and that stronger female choice tends to favor lower male  $F_0$  and more  
341 modest size dimorphism among polygynous primates. It is also possible that the unprecedented  
342 lethality imbued to human fighting with the advent of handheld and projectile weapons elevated  
343 the importance of threats and deference in relation to physical attacks (52, 57). Finally, in  
344 arboreal primates, large body mass may impose additional energetic costs, as well as  
345 increasing the risk of injury from falls. Although the relatively limited number of species in our  
346 sample prohibited exploring interactions between mating system, habitat, and body mass  
347 dimorphism, we note that the single species in our sample with the greatest  $F_0$  dimorphism,  
348 *Cercopithecus campbelli*, is polygynous, partly arboreal, and exhibits body mass dimorphism  
349 comparable to that of humans. In other words, one can speculate that male *C. campbelli*  
350 achieve polygyny partly via acoustic threats and/or mate attraction while body mass is  
351 constrained by partial arboreality.

352           In many species, males exaggerate size to intimidate conspecifics, but attention to these  
353 exaggerations is likely maintained by a continued association between apparent size and



354 formidability (4). Although  $F_0$  decreased with increasing body size in both sexes across primate  
355 species, body size only weakly predicts  $F_0$  in adult humans (5, 7). However, our data show that  
356 cortisol and testosterone interact to predict men's  $F_0$  in a pattern that has previously been found  
357 to predict men's dominance (35), attractiveness (34), and immunocompetence (34), and hence  
358 that  $F_0$  is likely to reveal male condition to same-sex competitors and potential mates.

359 Our results thus not only demonstrate a likely influence of sexual selection in the origins  
360 and maintenance of sexual dimorphism in  $F_0$  across anthropoids, but also suggest that male  
361 contests, and to a lesser degree female mate choice, favor low male  $F_0$  as a signal of condition,  
362 shedding new light on the intensity and mechanisms of sexual selection in humans and other  
363 primates. Future research should extend these comparative investigations to vocal tract  
364 resonance frequencies, which have been implicated in mating competition and size  
365 exaggeration in several mammals (1, 4, 7), including humans (11, 15).

366

367 **Ethics.** Participants provided informed written consent. The ethics committees of Michigan  
368 State University and The Pennsylvania State University approved these studies, and all  
369 procedures adhered to the Declaration of Helsinki.

370

371 **Data accessibility.** Data deposited in Dryad Digital Repository:

372 <http://datadryad.org/submit?journalID=RSPB&manu=RSPB-2015-2830>

373

374 **Authors' contributions.** Conception and design of the experiments: DAP, AKH, RAC, RPB;  
375 collection, analysis, and interpretation of data: DAP, AKH, DHB, RSW, DR, JRW, LLMW, RPB,  
376 ARL, CLA, MJO, CB, MEG, GR-F; drafting the article or revising it for important intellectual  
377 content: DAP, AKH. All authors approved the final version of the manuscript.

378

379 **Competing interests.** We declare we have no conflict of interest.

380

381 **Funding.** DAP was supported by a National Institutes of Mental Health T32 MH70343-05  
382 fellowship. JRW was supported by a National Science Foundation predoctoral fellowship.

383

384 **Acknowledgements.** This paper is dedicated to our colleague and friend, Michael  
385 Owren, an exemplary scientist and human being. We thank Robert Montgomerie,  
386 George H. Perry, David Reby, and two anonymous reviewers for comments on previous  
387 drafts of this manuscript.

388

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532



533 **Figure Legends:**

534

535 Fig. 1. Phylogenetic tree of anthropoid primates included in Study 1 for which data were  
536 available on at least 2 vocalizations from each sex (mean number of vocalizations: females =  
537 38.6, males = 22.1; max: females 181, males = 155; Table S1). Tree was constructed using a  
538 consensus phylogeny for all species in our sample from the 10kTrees website  
539 (<http://10ktrees.fas.harvard.edu/>). Sexual dimorphism (male/female) in  $F_0$  is shown in the  
540 column to the left of species names. Inferred ancestral states were determined using squared  
541 change parsimony and are shown at nodes on the tree (colored to highlight evolutionary trends).

542

543 Fig. 2. Sexual dimorphism in vocal  $F_0$  as a function of mating system. In panel (a), data points  
544 represent individual species, and horizontal bars represent mean  $F_0$  dimorphism for each mating  
545 system. Sexual dimorphism in  $F_0$  is most extreme in polygynous anthropoid primates and lowest  
546 in monogamous species. This remains true after adjusting for body mass dimorphism (b), and  
547 after adjusting for both body mass dimorphism and phylogenetic non-independence (c). Panel (c)  
548 shows results from phylogenetic generalized least squares regression with statistics for the  
549 effect of mating system on  $F_0$  dimorphism. In panels (b) and (c), least-squares regression lines  
550 with 95% CI are plotted, mating system refers to polygyny (coded as -1) vs. monogamy (coded  
551 as 1), and adjusted values are residuals after each variable was regressed on body mass  
552 dimorphism. Key for independent contrasts in panel (c) is shown in panel (d).

553

